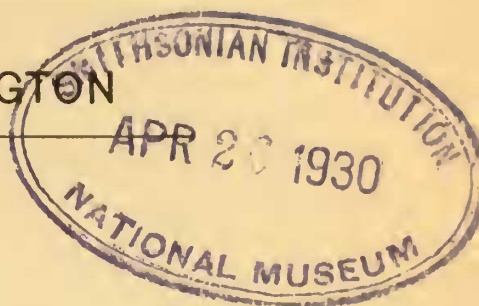# PROCEEDINGS

OF THE

## BIOLOGICAL SOCIETY OF WASHINGTON

# CONCERNING THE STRUCTURE, FUNCTION, AND ORIGIN OF THE CORNICLES OF THE FAMILY APHIDIDAE.

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## INTRODUCTION.

The Homopterous family Aphididae has long been looked upon as furnishing abundant favorable material for investigation. The peculiar method of reproduction of the family seems to have received extensive and careful consideration by the early investigators. It was while pursuing this line of research, no doubt, that attention was directed to the form and function of the cornicles, structures which so fundamentally separate aphids from all other insects. It is not surprising that sensory, respiratory and excretory functions should have been attributed to such conspicuous and unique structures as the cornicles by the early workers. Morphological studies on the internal structure of the cornicles had to wait until suitable histological technique was developed. Since such technique has been perfected, few students have applied it to the study of the cornicles. Therefore, our knowledge of their internal structure is extremely limited, and as a consequence of this, the significance of the internal structure of the cornicles has never been fully appreciated. Emphasis has been placed upon their external form alone, ignoring the fact that it is the internal functional portion of the cornicle that is the more fundamental.

This study has been attempted with the view in mind of explaining what the cornicles are, what they do, and from what

structures they may be traced phylogenetically.   This has been done in order to arrive at a better understanding of their value as characters useful in the classification of the family Aphididae, the application of which is left to the future.

### Part I.   Structure.

Cornicles may best be described as a pair of tube-like structures which are situated on the dorso lateral surfaces of the sixth abdominal segment of most species of Aphididae.   Because the external form of the cornicles is given to considerable variation, they have long been recognized as useful taxonomic characters.

In general, it may be said that the external portions of the cornicles present five distinct types.   The procornicular type (fig. 1), the tuberculate (fig. 2), the truncate (figs. 3, 4), the cylindrical (figs. 5–9), and the pore-like (figs. 10, 11).   The procornicular type of cornicle, as represented by the cornicles of the genus Monellia is a very primitive type, heretofore not recognized as such.   Cornicles of this type differ but slightly from lateral tubercles, which are rudimentary structures, and usually functionless.   In the tuberculate type of cornicle, the cornicle proper is situated upon a tuberculate or volcano-shaped area of the body.   Cornicles of this type are characteristic of the tribe Lachnini.   The truncate type of cornicle is well exemplified by the cornicles of species belonging to the tribes Chaitophorini and Callipterini.   In these tribes, the cornicles are rather truncate or trunk-like in shape, and as a rule are no longer than they are wide at the base.   Cornicles of species belonging to the tribe Chaitophorini are often more or less irregularly reticulated, the reticulations in this case being of the same nature as the reticulations found on the body.   Cornicles of species belonging to the tribe Callipterini are characteristically never reticulated, although in some species they may be modified by being somewhat swollen at the base.   Cylindrical cornicles are usually much longer than wide.   Tuberculate and truncate cornicles show but comparatively few modifications, but cornicles of the cylindrical type are given to exceedingly great external variation.   In general, cornicles of this type are long, more or less movable tube-like structures in contrast to the short fixed cornicles of the Lachnini, Chaitophorini, and Callipterini.

Cornicles, regardless of type, always have at or near their apical end an opening which is usually in the form of a semi-circular slit.   This opening is of primary importance, because it is actively concerned with the internal function of the cornicles.   The slit is so constructed that it may be opened and closed by a valve which is moved by a muscle attached near the median, free portion of the valve.   The valve muscle has its insertion in the ventral portion of the body wall.   The valve is usually attached for a short distance around the rim of the cornicle by a flexible hinge.

Cornicles of the long cylindrical type are at least somewhat movable. This presupposes some sort of a moving mechanism.   Flögel mentions and figures such (fig. 13).   I have not been able to locate the muscles found by Flögel either in cross or frontal sections, and suggest that the

valve muscle may perform a double function, since the cornicles are but slightly movable.

The literature of the structure of the cornicles is scarce and on the whole not very satisfactory. Few workers have based their observations on sectioned material. They seem to have depended largely upon gross dissection and upon the clearing and mounting of specimens in toto, processes not lending themselves to accurate interpretation. No comparative study of the internal structure of the cornicles seems to have been made. My study of the embryology of the cornicles, while fragmentary and not intended as a comprehensive treatment, adds a little to our knowledge of their development, and is apparently the first based upon sectioned material.

The external portion of the cornicles is derived from the ectoderm. That the comparatively little known internal portion is derived from the same germ layer as the external portion of the cornicle, has been taken for granted, for all authors except Witlaczil so consider it. Witlaczil believed the internal portion of the cornicles to be derived from the mesoderm, and the evidence furnished by my sections so indicates. The structures described by Sulc as being present in *Pseudococcus farinosus* DeGeer are certainly suggestive of the internal structure of the cornicles of certain species of aphids. Sulc looked upon the cells which he found as being degenerated fat tissue which functioned in the defense of the organism. Without considering the function of these structures, but judging them solely by their structure, it would appear that Sulc was justified in declaring them homologous to the cornicles of the family Aphididae.

The structure of the cornicles of the genus Lachnus will be described first. Mordwilko, having sectioned *Tuberolachnus viminalis* Boyer (considered at that time to belong to the genus *Lachnus*) appears to have been the first worker to make a histological study of cornicles of this type. I have not had material of this species to section, but my interpretation of the structure of the cornicles of two typical species of the genus *Lachnus* differs somewhat from Mordwilko's interpretation.

STRUCTURE OF THE CORNICLES IN THE EMBRYO OF LACHNUS COLORADENSIS GILLETTE (Figs. 14–16). Before there is any indication of a tubercle in the locality where the cornicles will shortly manifest themselves there appears beneath this area a rather finely granulated nucleus in a mass of greatly vacuolated tissue, usually more or less intimately associated with fat cells. Such nuclei are usually larger than any nuclei found within the body cavity. The cytoplasm of the glandular mass, although greatly vacuolated, presents a very homogenous appearance. These vacuoles are apparently empty spaces which were once filled with secretory substance.

STRUCTURE OF THE CORNICLE IN THE ADULT OF LACHNUS COLORADENSIS GILLETTE (figs. 17–19). The chitin covering the tubercle appears to be considerably thicker than the chitin covering the outer portions of the body. The cornicle itself is short. A narrow, flat brim extending slightly downward is found at the apex. The valve is not set flush with the outer margin of the cornicle but is somewhat sunken or depressed. The chitin

to which the valve is fastened extends downward for a short distance within the cornicle and then bends back upon itself, thus forming a rather flexible hinge.   The valve fits up against an inwardly projecting portion of the rim of the cornicle, enabling the opening to be completely closed. Within the tubercle is found a large, nucleated glandular mass consisting, apparently, of two kinds of cells, which for convenience will be distinguished by the letters A and B.   The cytoplasm of the A type of cell, which takes a dark stain, is coarsely vacuolated, the vacuoles varying considerably in size.   Large granular nuclei are scattered at random throughout the cytoplasm.   There are no cell boundaries.   Cells of this type are usually found close to the valve.   The B type of cell is much more delicate in structure. They may surround three sides, or may lie directly beneath the glandular mass made up of the A type of cell.   Cells of this type are greatly vacuolated, the vacuoles being small and uniform in size.   There are no cell membranes apparently, separating cells of the B type, but the limits of the individual cells may in some cases be distinguished.   The B type of cell fills the greater portion of the cornicular cavity.   I regard the cavity or cavities often seen at the extreme inner portion of the tubercle as artifact. It is this cavity which I think Mordwilko interpreted as the wax sac. The wax sac of Mordwilko could be derived by a shrinking or disintegrating of the cells in the interior, leaving only a membrane-like residue toward the outside containing nuclei.

Mordwilko mentions the fact that the cells on the inner side of the valve are larger than those forming the hypodermis proper, and concludes that they are glandular in function.   I agree with him that they are larger than the ordinary cells of the hypodermis, but not perhaps to the extent that Mordwilko's figure of them would lead one to expect (fig. 20).   I do not agree with him that these cells are glandular in function for they certainly exhibit none of the characteristics of active glandular cells.   They appear to be slightly modified hypodermal cells, since they differ only in the matter of size.   At the margin, away from the attachment of the valve, the valve muscle attaches itself.   At this point, there is an almost imperceptible transition from the hypodermal cells to the cells of the muscle proper.   The valve muscle runs backward and downward to attach itself near the median line on the ventral side of the abdomen.   From sections it is impossible to tell precisely the segment to which it attaches itself, but it would appear to be the segment posterior to the cornicles, and according to Mordwilko it is.

The cornicles of Longistigma caryae (Harris).   The cornicles of this species are very similar to the cornicles described for the genus *Lachnus*. The glandular portion is apparently considerably larger than that found in the genus *Lachnus*, while the cells of the A type are not as numerous.

The cornicles of Eulachnus agilis (Koch).   The oviparous females of this species were sectioned.   Externally, the cornicles of this species are greatly reduced; internally, they depart widely from the cornicles of the genus *Lachnus*.

The Cornicles of Monellia caryella (Fitch).   Internally, the cornicles of *Monellia caryella* differ in many respects from the cornicles of

other genera. By virtue of the active, functioning cells, which are intimately united in a glandular mass resembling a small sac closely associated with the valve, these cornicles appear most closely related structurally to the cornicles of the genus *Lachnus*.

STRUCTURE OF THE CORNICLE IN THE EMBRYO (fig. 21). The information pertaining to the structure of the cornicles in the embryo is based upon rather meager material representing somewhat mature embryos of approximately the same age. There is apparently no thickening of the hypodermis in the vicinity of the two hollow, ball-like structures found in the posterior lateral portions of the abdomen. These structures in section resemble hollow rings, and are the first indication of the developing cornicles. In the embryos studied they were already well developed. Nuclei are to be found within the band, while the area within is clear and apparently empty, indicating that at this stage it was already filled with secretory substance. There appears to be no internal membrane, and because the internal surface is rather uneven, it is very doubtful if such a membrane is present. No sections show the opening of the cornicles or the muscle operating the valve. This, however, is not surprising, for even in the adult the external portion of the cornicle is difficult to find.

THE STRUCTURE OF THE CORNICLE IN THE ADULT (fig. 22). The internal portion of the cornicle consists of a sac-like, glandular tissue in which the cytoplasm is differentiated into three regions; there is an open, sac-like region next to the mouth of the cornicle, which in life may have been filled with secretory substance. This region is surrounded by a deeply staining mass of vacuolated cytoplasm containing nuclei. This, in turn, is surrounded by a layer of cytoplasm which takes the stain to a much less degree than the former. Since no cell membranes may be distinguished, and in as much as there are no nuclei present, except in the darker staining inner portion, the various regions will have to be interpreted as differentiated areas of the cells making up the inner portion of the cornicle. The nuclei are large and stain deeply. Near the mouth of the cornicle a muscle attaches itself to a rather sloping valve. The valve muscle runs downward as well as backward, presumably to find its insertion in the ventral body wall.

THE STRUCTURE OF THE CORNICLES IN SYMYDOBIUS AMERICANUS BAKER.

STRUCTURE OF THE CORNICLE IN THE EMBRYO (figs. 23, 24). No embryos show the cornicles in their early stages of development. A small embryo shows a hollow structure of glandular tissue not unlike that mentioned for the genus *Monellia* in the embryonic stage. Near the outer margin of the glandular mass it lies close to the slightly thickened hypodermis. Several embryos show one or two smaller glandular masses near the larger ones, but these are apparently of the same nature. Another embryo which seems to be almost mature, shows the glandular mass in contact with the hypodermis, which at this point is greatly thinned. The nuclei in this thinned area are absent.

THE STRUCTURE OF THE CORNICLES IN THE ADULT (fig. 25). The valve, which opens towards the anterior end of the body, is situated about one half of the way down the cornicle, and is set at a rather sharp angle.

There is a slight thickening on the opposite wall of the cornicle so that when the valve fits up against it, the opening is tightly closed. The valve muscle attaches to the free end of the valve and runs downward and backward to attach itself to the ventral body wall. The glandular sac is large, and is usually oval or oblong in shape. Along the wider and longer portions of the sac the walls consist of a single layer of vacuoles surrounded by a homogeneous, deeply staining cytoplasm in which the nuclei are situated. At the ends of the sac there may be several rows of vacuoles present. Large, deeply staining nuclei are found in the walls of the sac. One or two individuals show smaller, glandular, sphere-like sacs similar to those mentioned as being present in the embryo. The large sac does not join directly with the opening made by the valve, although it may extend up into the cavity of the cornicle and thus approach it. The fact that some specimens show smaller sacs in addition to the larger one may indicate that the cornicles of this species are in what may be called a transition stage between the cornicles of the myzocallis type and the cornicles of the genus *Aphis.*

THE CORNICLES OF THE GENUS NEOTHOMASIA. The oviparous females of *Neothomasia populicola* (Thomas), and the viviparous females of *Neothomasia abditus* Hottes were sectioned. In general, the cornicles of this genus differ but slightly from the structure of the cornicles of *Symydobius americanus.*

The cornicles of *Callipterinella betulaecolens* (Fitch) and *Myzocallis bellus* (Walsh) are similar structurally to the cornicles of *Symydobius americanus* except that they do not show small, sphere-like sacs in addition to the larger one. (Figs. 26, 27.) The cornicles of *Calaphis betulella* (Walsh) occasionally show small spheres.

It is suggested that the valve of the genus *Symydobius,* in the process of being drawn in, drew in also that portion of the cornicle which ordinarily enters into the formation of the rim.

THE STRUCTURE OF THE CORNICLES OF ANOECIA OENOTHERAE WILSON. Only poor sections of *Anoecia oenotherae* were obtained. Provisionally, it would seem that the cornicles of this species conform more closely to the cornicles of the genus *Neothomasia* than they do to the cornicles of the genus *Lachnus.* This fact suggests that the genus *Anoecia* may not be as closely related to the Lachnini as has been thought.

THE STRUCTURE OF THE CORNICLES OF DREPANAPHIS ACERIFOLII (THOMAS). The cornicles of this species differ from those heretofore described in this paper. They seem to represent the phylogenetic goal towards which the internal structure of the cornicles has been directed.

THE STRUCTURE IN THE EMBRYO. In this genus, it is the internal structure again, which first makes its appearance. The first indication of the cornicles was found in rather mature embryos. At this stage a number of hollow spheres, consisting largely of vacuoles surrounded by cytoplasm, may be seen near the posterior lateral margins of the abdomen. Each sphere consists, apparently, of but one cell; there is but one nucleus present.

No embryos show any indication of the external portion of the cornicle.

THE STRUCTURE OF THE CORNICLE IN THE ADULT. Within the body

cavity in the vicinity of the cornicles and within them, numerous hollow and partially hollow spheres may be seen, each containing a single nucleus. If the spheres are hollow, the outer surface is only one vacuole thick. If not they appear to be partially filled with vacuoles separated from each other by a net work of cytoplasm. These spheres are tightly compacted within the cornicles, but within the body cavity they present a somewhat looser arrangement. In general, they bear a striking resemblance to the loose, small spheres present in the genus *Symydobius*. The solid spheres show a somewhat distant resemblance to fat cells, from which they may be separated quite easily by their nuclei. Their cytoplasm is more uniformly vacuolated than the cytoplasm of the fat cells and takes a darker stain.

The cornicles of the genus Melanoxantherium (fig. 28). Two species belonging to this genus were sectioned, *Melanoxantherium salicis* (Linnaeus) and *Melanoxantherium smithiae* (Monell). Internally, both in adult and embryo, the cornicles of this genus are suggestive of the cornicles of the genus *Drepanaphis*.

The cornicles of the group Macrosiphini (fig. 29). Species belonging to the following genera were sectioned: *Acyrthosiphon, Microsiphum, Macrosiphoniella, Catamergus*, and *Tritogenaphis*. The species of this group present but minor differences as far as the internal structure of the cornicles is concerned, from the cornicles of the genus *Drepanaphis*. The number of spheres varies greatly. Sometimes they are so numerous that they extend across the posterior end of the body joining those in the vicinity of the cornicle on the other side. At other times they are very limited in number.

The cornicles of the tribe Aphidini (fig. 30). Species of several genera belonging to the tribe Aphidini were sectioned. The cells at the base of and within the cornicles of *Thargelia albipes* (Oestlund) differ enough from the cells thus far described to warrant a description. The cells found here are somewhat suggestive of oenocytes from which they may be easily separated by their small size, evenly vacuolated cytoplasm, and the manner in which they stain.

The structure of the cornicles of Schizoneura lanigera (Hausmann). My interpretation of the structure of the cornicles of this species differs from the interpretation of Baker and Davidson, and is more in line with what one would naturally expect knowing the structure of the cornicles in other species belonging to the family. Because of this discrepancy, further sections will be made before publishing.

### General Consideration of Internal Structure.

On the basis of internal structure, two types of cornicles may be considered. In the primitive type, the glandular mass has a direct connection with the outside, as is the case in the cornicles of *Monellia* and *Lachnus*. The more modern type of cornicle has an indirect connection between the glandular mass and the cornicular opening, and is well illustrated by cornicles of the Macrosiphini and Aphidini. Cornicles having an indirect connection are of two kinds: those having mononuclear sacs or spheres,

as for example the cornicles of Macrosiphini and Aphidini; and those having a polynuclear sac, as for example the cornicles of the genus *Symydobius*. The mononuclear spheres are apparently derived by a breaking up of the polynuclear sac, and are therefore homologous to it.

<div align="center">Part II. The Function of the Cornicles.</div>

Reaumur, who appears to have been the earliest worker to make an extensive study of the family Aphididae assigned to the cornicles for the first time a function, although a function had been implied by Von Frisch in his designation of them under the name of Fühlspitzeln. Reaumur regarded the heavy, dark colored liquid which came from the tips of the cornicles as analogous to the feces of other animals, and the liquid from the anus as analogous to urine.

Bonnet, a follower and reported student of Reaumur, first considered the cornicles to function in the production of honey dew; later, however, he considered the cornicles to function as urinary organs. Bonnet looked upon the pulverulent matter often seen on the bodies of aphids as being of the same nature as the material given off by the cornicles. He took it to be a kind of perspiration having a great similarity to urine, which he thought found its way to the surface of the body by means of numerous small pores.

Linné followed the first view held by Bonnet, and believed that the cornicles functioned in the secretion of honey dew.

Rev. Kyber thought that aphids would soon bury themselves by their own feces, if the function of the cornicles was excretory, and therefore assigned to them two functions. First, that they were breathing pores, a theory held by several subsequent workers. His second theory seems to have figured but little in literature. Briefly, he thought it not unlikely that the cornicles functioned as levers by means of which the aphids could more easily raise the hinder part of the abdomen when the cornicles were inclined towards the head.

Charles Morren declared the cornicles to be prolonged stomata. He believed the cornicles to have a second function; that of secreting the honey dew which he regarded as being the first food of the young, since he repeatedly saw young aphids suck the secretions fron the tips of the cornicles.

Kaltenbach considered the cornicles to be respiratory in function. He looked upon them as organs necessary for the rapid oxidation of food matter, a condition brought about by the rapid vital functions carried on by the individuals of this family.

Buckton, after reviewing all previous theories as to the function of the cornicles regarded them as excretory ducts, from which oily globules were passed from time to time, thus removing material which would cause the death of the individual if allowed to accumulate. Buckton, however, perpetuates the idea that ants gather honey dew from the cornicles, for in one of his plates he shows an ant in the act of receiving a drop of honey dew from the tip of one of the cornicles of *Aphis sambuci* L.

Witlaczil in his first paper written in 1881 designated the cells found in

the cornicles and in the vicinity of their base by the name of sugar cells (Zuckerzellen). These cells, he thought, were given off through the medium of the cornicles, and as evidence of this he cited the empty spaces found at the base of the cornicles of adult aphids. Witlaczil, however, recognized that the honey dew came from the anus. In his second paper published in 1882 Witlaczil retained the view brought out in his first paper, but in his third paper published in 1884 he regarded the cells found at the base of the cornicles as having a urinary function.

Büsgen was the next worker to offer a function for the cornicles. His theory has been widely accepted by entomologists, and is the one offered by most present day workers who venture an opinion. Büsgen considered the cornicles to be wax producing glands which function as organs of defense against predacious enemies.

To recapitulate, the theories brought forward in regard to the function of the cornicles may be broadly classified as excretory, respiratory and protective.

The theories held for the function of the cornicles by Kyber, Linné, Morren and others have long since become a matter of history. The protective theory even as long ago as 1908 was rather severely questioned by Gillette, who at that time doubted if a secretion which did not often free itself from the cornicles could be very effective in defending aphids from the attacks of predaceous and parasitic insects. Several others, while doubting the effectiveness of the cornicles as organs of defence, have failed to publish their opinions, or have referred to them merely as excretory ducts.

When the cornicles are considered critically from their internal structure, form and performance, it becomes evident that they are not well adapted to perform effectively the function of protection. The cornicles at their best are but slightly movable, thus making the possibility of their being aimed in all directions practically nil. While the amount of secretory substance appears to be ample in all species, it is seldom that more than a single drop may be coaxed to the tip of the cornicle. The droplet coagulates immediately, retaining the shape of a small sphere, and has no tendency whatever to spread. Thus, should it ever leave the tip of the cornicle, there would be great need of effective placing in order to glue up the mouth parts of the enemy. It has been said that aphids would expel droplets from the cornicles when confronted by their enemies. It has been my experience, however, that aphids are not easily frightened, and that they remain unconcerned even while being walked over by those who are in the habit of feeding upon them. Droplets may, however, be brought to the surface of the cornicles by pressure applied to the body of the aphid. In nature, this pressure naturally is produced by the aphid's enemy at the moment of grasping the aphid between its mandibles. The droplets must, therefore, be looked upon as a result of pressure, and not as a result of the desire of the aphid to defend itself. The large glandular masses present at the base of the cornicles of the Lachnini indicate that the function of the cornicles is of a physiological nature.

From the location of the internal portion of the cornicles, which is

bathed on all sides by the body fluids, it is suggested that the cornicles may function in connection with some of the metabolic processes carried on by the individual.   If this is true, the product is of an excretory nature, given off in the form of a gas at the mouth of the cornicle.   Morphologically, the structure of the cornicles is of such a nature that volatile matter could be given off, if it were present, and if it were necessary for it to be removed.   The valve is ideally constructed for such a purpose.   The internal portion of the cornicle is close enough to the mouth of the cornicle so that volatile matter would not be greatly hampered in making its escape. It is known that the material within the cornicles coagulates or hardens immediately upon coming in contact with the air, and it may be deducted from this, that there is constituent within it which is highly volatile.

If the function of the cornicles is excrétory as has been suggested, the source of the volatile matter will have to be accounted for, and the reason for its not being taken care of by ordinary means explained.   Structure, when taken alone, indicates the degree of functional development which an organism or organ has attained.   Differences in structure may therefore be taken as indicative of the variability and complexity of function. The variation in the internal structure of the cornicles may therefore be taken as an indication that the factors entering into their function are variable.   This is what one might expect, knowing something of the biological habits of the family.

Aphids have, perhaps, established a closer, more continuous, and a more intimate relationship with their hosts than any other ectoparasitic insects.   This relationship has had its effect upon their mode of reproduction, their early maturity, and their reproductive capacity—all of which are highly characteristic of the family.

Büsgen's data showing the amount of honey dew produced per aphid in twenty-four hours would lead one to believe that the taking in of food has become an almost continuous process.   Indeed, they appear at all times to have their beaks inserted in the tissue of the host, and to withdraw them only upon being disturbed.   Early maturity and the development of a large number of young are processes which require a vast amount of food, so that the continuous feeding habit is not at all surprising.   However, this food must be properly balanced.   The large amount of waste material given off in the form of honey dew by the aphids indicates that the sap upon which they feed is limited in some element which is probably protein, which can be obtained in necessary amounts only by taking into the digestive system an excessive amount of sap which is composed largely of carbohydrates.   The sap of plants is known to be a very complex substance. Certain of these sap products must be incapable of being assimilated, and made use of even though they enter into the blood stream of the aphid. These products must be removed by the glandular internal structure of the cornicles or by some other means.   It is well known that the constituents making up the sap content of various plants differ.   Since the amount of food consumed by aphids is comparatively large, and since there is some evidence showing that aphids have evolved along with their hosts, it is not at all surprising that related groups should have responded in a similar

manner to a similar stimulus; a stimulus not faced to such a marked degree by other insects whose food is not so limited as to kind, and where the consumption of it is not a continuous process. The loss of the cornicles must be accounted for by a change in the factors making them necessary. Their absence can be correlated with certain morphological and biological characteristics such as the presence of wax pores, the absence of cauda, low reproductive rate, and a slower rate of development which as a consequence decreases the number of generations per year. The biological factors indicate that the groups without cornicles have failed to maintain what may be called a degree of plasticity between the organism on the one hand and its host relations on the other. The slowing up of the biological processes may be interpreted as a direct result of this. Therefore, any change in the structure of the cornicles must be a result of the nature of the food consumed by the individual because this alone can affect the functional portion of the cornicle.

## PART III. THE ORIGIN OF THE CORNICLES.

In attempting to account for the origin of the cornicles, one may proceed in either of two directions. He may choose to look upon the cornicles as organs *de novo*. If he does so, he is immediately confronted not so much by the question how they arose, but how many times, for species with and without cornicles are found in all of the major groups of the family. Or he may proceed to derive the cornicles from and through modifications of preexisting structures. Since the cornicles are found well developed, even in the more generalized forms, and are apparently lacking only in those forms which have greatly modified their biological processes, it may be concluded that the cornicles arose only once.

Since the cornicles are such unique structures in the class Insecta, it is not surprising that structures with which they may be readily homologized are lacking. Examining the order Homoptera of which the family Aphididae is a member, one is immediately impressed by the well developed dermal glandular system, a system which certain aphids have retained, and a system which certain others show evidence of having once had.

The period of time during which the cornicles were undergoing their development may be divided into two epochs. A precornicular epoch and a cornicular epoch. A generalized dermal glandular system may have taken care of the function which is now performed by the cornicles in the progenitors of the family Aphididae. Such glands were undoubtedly arranged in six longitudinal rows, four dorsal and two marginal. This is quite evident from the arrangement of the wax glands and a somewhat similar arrangement of the tubercles and of the glandular and sensory hairs when they are present. During this time there was no differentiation either in structure or function between the glands on the dorsum and the glands on the lateral margins of the body. We may consider the first stage in the development of the cornicles to have been reached when a differentiation in structure and function took place between the glands on the dorsum and the glands on the lateral margins. We have examples of this in

Forda and Anoecia and a few other genera where the lateral glands no longer function in the same manner as those found on the dorsum. In the second stage of the development of the cornicles, which brings to completion the precornicular epoch, the lateral glands became lateral tubercles.

From sections, I am convinced that lateral tubercles and lateral glands are the same functionally. In fact, they do not differ fundamentally in structure, except that the former have become tubercles. In certain forms, the lateral tubercles are filled with large glandular cells which appear to be nothing other than greatly modified cells of the hypodermis. The cell cytoplasm is not greatly vacuolated. The nuclei are large and finely granulated. Apparently there are no pores in the chitin covering the tubercles in the vicinity of the gland cells. Pores leading to the outside may exist, but a careful search fails to reveal them. Two kinds of lateral tubercles may be distinguished in the family. One in which the lateral tubercles are filled by active, functioning cells and the other where the tubercles are filled with mesodermal tissue. Lateral tubercles where the cells have been lost appear to be the rule in the Calliperini and Calaphidini. In many species belonging to these tribes, the lateral tubercles are almost as well developed as the cornicles. A few species belonging to the tribes just mentioned bear on the sides of the lateral tubercles, window-like areas now covered over by chitin (fig. 12). Such areas are very suggestive of the terminal openings of the cornicles, and become very significant when considered as homologous structures of the terminal openings, now covered over. These structures are not found at the tips of the tubercles, but are to be looked for on the posterior side. This location may have been the original position of the cornicular opening; if so, it has been retained by but few species belonging to the family (fig. 7).

Just previous to the cornicular epoch we may suppose that certain lateral tubercles became more efficient than others. The centralization of function which seems to have been ever present and ever active, continued until finally one pair of tubercles which may now be called procornicles was performing the function once performed by several pair. The tubercles on certain segments seem to have been more persistent than others. With the exception of the tubercles found on the seventh abdominal segment, those tubercles which are furtherest away from the disturbing influence of the cornicles, such as those on the prothorax, and those on the first, second and third abdominal segments are the most common. This indicates that the cornicles did not become dominant all at once. The external portion of the cornicles at this time had not yet begun to change its form. Such a condition is met with in the genus *Monellia* and a few other genera in which the external portion of the cornicles is so feebly developed that they could easily be taken for lateral tubercles were it not for the presence of terminal openings.

The intimate relationship which exists between the internal functional portion of the cornicle, and the external portion, particularly the valve, presupposes that the two portions underwent their evolution during similar epochs. If this is so, one would not expect to find a high type of internal structure, such as is found in the group Macrosiphini, present in

cornicles belonging to the procornicular type; neither would one expect to find cornicles which belong internally to the type found in the genus *Lachnus*, present in cornicles which belong externally to the cylindrical type. The present status of our knowledge of the internal structure of the cornicles bears this out.

Our knowledge of the internal structure of the cornicles is at present too limited to draw a complete picture of their phyolgenetic development without relying rather strongly upon the evidence furnished by their external form. For example, a wide gap exists between the glandular mass type of cornicle and the polynuclear sac type, when the two are considered on the basis of their internal structure. When the two are considered on the basis of their external form, this gap no longer exists, for the truncate type of cornicle may be derived from the tuberculate type by a narrowing down of the tubercle. There is evidence to show that the mononuclear spheres were derived by a breaking up of the polynuclear sac. Externally cylindrical cornicles, which are internally characterized by mononuclear spheres, may be derived from truncate cornicles, which internally are characterized by a polynuclear sac, by a process which tends both to thin and lengthen the truncate cornicle.

## EXPLANATION OF PLATES.

Fig. 1. Procornicular type of cornicle.
" 2. Tuberculate type of cornicle.
" 3. Truncate type of cornicle.
" 4. Truncate type of cornicle.
" 5. Cylindrical type of cornicle.
" 6. Cylindrical type of cornicle.
" 7. Cylindrical type of cornicle.
" 8. Cylindrical type of cornicle.
" 9. Cylindrical type of cornicle.
" 10. Pore-like type of cornicle.
" 11. Pore-like type of cornicle.
" 12. Lateral tubercle showing "window."
" 13. Figure taken from Flögel showing muscles for the movement of the cornicles. rö. die horizontal liegende Röhre, ar. arrector tubuli, mr. musculus valvulae, do. Dorsoventralmuskel, pi. Pigmentflecke, st. Stigma.
" 14. Longitudinal section of cornicle through embryo of Lachnus coloradensis Gillette.
" 15. Cross section through embryonic cornicle of Lachnus coloradensis Gillette.
" 16. Section through embryonic cornicle of Lachnus coloradensis Gillette.
" 17. Longitudinal section through the cornicle of Lachnus coloradensis Gillette. (Composite.)
" 18. Longitudinal section through the cornicle of Lachnus coloradensis Gillette. (Composite.)

Fig. 19. Cross section through the cornicle of Lachnus coloradensis Gillette.

" 20. Figure taken from Mordwilko, showing a section through the cornicle of Tuberolachnus viminalis Boyer. sh. Safthocker, hd. Deckel des Safthockers, dz. Region der höhen Drusenzellen, wh. Membran welche die flussig wachartige Masse weinschlieszt, br. m. grobkornige rothbraune Masse, r. m. dorsoventraler Respirationsmuskel, mt. r. Hypodermis.

" 21. Longitudinal section through the embryonic cornicle of Monellia caryella (Fitch).

" 22. Longitudinal section through the cornicle of Monellia caryella (Fitch). (Composite.)

" 23. Longitudinal section through embryonic cornicle of Symydobius americanus Baker.

" 24. Longitudinal section through embryonic cornicle of Symydobius americanus Baker.

" 25. Longitudinal section through the cornicle of Symydobius americanus Baker. (Composite.)

" 26. Section through the embryonic sac of Myzocallis bellus (Walsh), the section to the right through the top of the sac, the section to the left just under the section to the right.

" 27. Longitudinal section through the cornicle of Myzocallis bellus (Walsh). (Composite.)

" 28. Section through the cornicle of Melanoxanterium salicis (Linnaeus).

" 29. Section through the cornicle of Microsiphum artemisiae (Gillette). (Composite.)

" 30. Section through the cornicle of Thargelia albipes Oestlund. (Composite.)